THE GENUS GEONEMERTES

BY CARL FREDERICK ABEL PANTIN WITH AN APPENDIX BY JANET MOORE Kufe

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Two New Zealand species of Geonemertes for comparison; above, G. pantini; below, G. novaezealandiae.

Photograph by Elizabeth J. Batham



THE GENUS GEONEMERTES

By C. F. A. PANTIN

FOREWORD

Among the late Professor C. F. A. Pantin's¹ papers was a manuscript "The Genus Geonemertes", written in 1952 but never published because of the influx of new material. At the invitation of Mrs. A. M. Pantin and Dr. J. E. Smith (Professor Pantin's scientific executor) Dr. Janet Moore has prepared the original manuscript for press by writing an appendix compiled from Professor Pantin's notes and correspondence (1952–66). The original manuscript required only very minor editing, and the appendix consists as far as possible of quotations from Professor Pantin's letters. There are, however, a few original observations and comments on the material. These are indicated in square brackets and initialled. The appendix also records the localities where various species have been found, and indicates the stage reached in various unfinished lines of research on which the account is based.

In putting this account together Dr. Moore has studied and become thoroughly familiar with the microscopic slides and specimens left by Professor Pantin and it is hoped that she will now continue the investigations where he left off. The slides and specimens are to be deposited in the British Museum (Natural History).

The illustrations have been drawn by Mr. W. B. Amos and are mostly based on sections selected and roughly sketched by Professor Pantin.

J. P. HARDING Keeper of Zoology

THE GENUS

IN 1937 Waterston and Quick recorded the occurrence of the terrestrial nemertine *Geonemertes dendyi* Dakin in South Wales. The subsequent discovery of many specimens in South Devon (Pantin, 1944) enabled me to make a study of this interesting organism ; a study which led to a consideration of the relationship of the species of the genus. This is of peculiar interest, because it concerns the one terrestrial genus of an almost exclusively marine phylum, and because several of the species occur in isolation on oceanic islands. It is this relationship of the species which we shall now discuss.

The characters of the genus have been summarized by Hett (1927), Brinkmann

¹ Professor Pantin, who died on 14th January, 1967, was at that time Chairman of the Trustees of the British Museum (Natural History).

(1947) and others. Inspection at once shows that the majority of these are no more than generalized metanemertine characters, particularly those of the relatively unspecialized families of the Tetrastemmatidae and Prosorhochmidae. Such characters are the single stylet, coincidence of mouth and rhynchostome, anteriorlydirected midgut caecum and the anterior diverticula of the intestine, the cerebral sense-organ. The only other common characters of all the described species are

- I. adaptation to terrestrial existence ;
- 2. the degenerate state of the head furrows (Kopffürchen) ;
- 3. the extensive development of the excretory system throughout the length of the body : for though the existence of such a system has been denied in many species it will be shown below that careful search always reveals its presence.

The first of these characters cannot of itself suffice to distinguish a genus without begging the question that it is not of polyphyletic origin ; a possibility which must be considered in view of the extraordinary distribution of the genus, and one which has been suggested more than once (Bürger, 1895 ; Brinkmann, 1947). The second and third characters might, as defined above, be no more than natural concomitants of adaptation to land life even if this took place several times independently : this is particularly the case since reduction of the head-furrows and development of the excretory systems have taken place on different lines in different species.

It is therefore necessary to consider the relationships of the species of the genus afresh. As Brinkmann (1947) points out, this is difficult because of the inadequate description of many of the species. He points out in particular how slender is our knowledge of the vascular and excretory systems, and suggests that these should not be employed in characterizing species because of the difficulty of observing them. Were this objection valid it would be very serious, for it is in just these systems that we may look for extensive and various adaptations to terrestrial conditions. Fortunately there is no doubt that when sections are cut in an appropriate plane (tangential to the surface) and stained with polychrome stains such as Mallory's triple stain, the major features of both these systems are easily seen even in indifferently fixed material. In the present work particular attention has been paid to these systems, and, in conjunction with other characters, they supply ample evidence to define the relations of many of the species of the supposed genus.

By good fortune I have been able to examine a number of the known species and thereby to add some significant facts about them. My survey has been based upon specimens and slides of *Geonemertes australiensis* Dendy in the collection of the late Professor Dendy at King's College, London : of *G. australiensis* Dendy, *G. hillii* Hett and *G. pelaensis* Semper¹ in the collection of Miss M. Hett : of *G. paelansis* Semper in the collection of Dr. Wesley Coe : of *G. rodericana* Gulliver from the British Museum : of *G. arboricola* Punnett from the Zoological Museum, Cambridge : of a specimen of *G. nightingaleensis* Brinkmann collected from Nightingale Island by the Norwegian Scientific Expedition 1937–38 : of specimens of *G. agricola* Willemoes-Suhm kindly collected for me by Dr. Brian Boden during the summer of 1951 in Bermuda : and of an undescribed specimen from Ceylon in the Cambridge Museum.

¹ This is often misnamed *palaensis* Semper.

These have been compared with specimens of G. dendyi collected by myself and, where necessary, with the freshwater *Prostoma graecense* (Böhmig) obtained from the River Cam (Braithwaite and Clayton, 1945), and with specimens of *Prosorhochmus claparedii* Keferstein from crevices near high water mark at Wembury and the Yealm, Plymouth. Professor Dendy's slides of G. australiensis were those on which his paper (1892) was based and his slides of G. novaezealandiae (Dendy, 1894, 1895) were restained and examined : Miss Hett's slides were those on which her papers on G. hillii and G. pelaensis were based (1924, 1927), and Dr. Wesley Coe's slides were those of his 1940 paper.

For reasons which will become apparent it is convenient to discuss first the Australian species, then those which I find to be related to G. *pelaensis*, and then to discuss the relation of the remaining species to these two groups.

The characters of the species

The relationship of species is determined by the number and by the quality of the

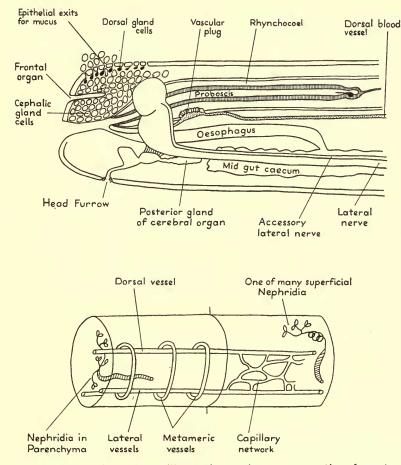


FIG. I. Anatomical scheme illustrating various geonemertine characters.

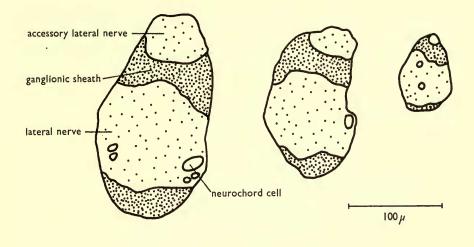
characters they possess in common. It is necessary therefore to appreciate the nature of the characters concerned. Some of the special characters upon which the argument of this paper turns are illustrated by Figure 1. The figure is diagrammatic and no one species possesses all the characters represented in it. Its sole, though important, purpose is to clarify the terminology used.

THE AUSTRALIAN GROUP

Let us first consider the species G. dendyi, G. australiensis and G. hillii. Dakin (1915) and Stammer (1934) have given incomplete accounts of G. dendyi, but the descriptions of the other two species by Dendy (1892) and Hett (1924) are fairly complete. My own observations have confirmed much of these descriptions and have added some new facts, particularly in G. dendyi.

In addition to their generalized metanemertine features the three species possess many special characters in common :

- 1. There is excessive multiplication of the four primitive metanemertine eyes over the rounded head—almost to an "ommatidial" condition with about twenty, forty and eighty eyes distributed over the head in the three species respectively.
- 2. The frontal organ, commonly present in nemertines, is absent in these species. This organ is a median anteriorly placed canal which in most nemertines receives the secretion of the cephalic glands (Fig. 1). In the three species we are discussing the secretion of these glands seems to escape to the exterior by extemporized channels through the basement membrane and epithelium of the head, as Dendy suggests in *G. australiensis*. I find this is true in *G. dendyi* (Figs. 9, 10) and re-examination of the slides of *G. hillii* shows the same thing.
- 3. "Dorsal gland cells" as described by Dendy (1892) and Hett (1924) are present. These seem to be integumentary glandular cells sunk below the muscle layer of the anterodorsal surface. They have a strong affinity for borax carmine and for orange G. in Mallory's triple stain (Fig. 9).
- 4. Arising from the dorsal lobe of the brain and running along the dorsal surface of the lateral nerve on each side is an "accessory lateral nerve"; a structure only found elsewhere in the genus *Oerstedia*, in the pelagic Polystilifera and some southern Tetrastemmatidae (Stiasny-Wijnhoff, 1930) such as *Tetrastemma* gulliveri (Bürger, 1893) (Fig. 2).
- 5. In G. australiensis and G. dendyi the cerebral organs are of similar structure and possess a large posterior glandular extension corresponding to the "oesophageal organ" of Dendy (Dendy, 1892) (Fig. 13). The duct from each cerebral organ runs forward and opens ventrally. Hett (1924), who compared the anatomy of G. hillii and G. australiensis, made no note of any difference in the structure of their cerebral organs and made no comment. My comparison of the original slides of both these species with sections of G. dendyi confirms the essential similarity of the whole cerebral organ in all three. Minor differences will be noted later.



hilliiaustraliensisdendyiFIG. 2. Camera lucida drawings of the lateral nerve in the three Australian species of
Geonemertes, just in front of anterior gut diverticula, to show the relative sizes of the
accessory lateral nerve.

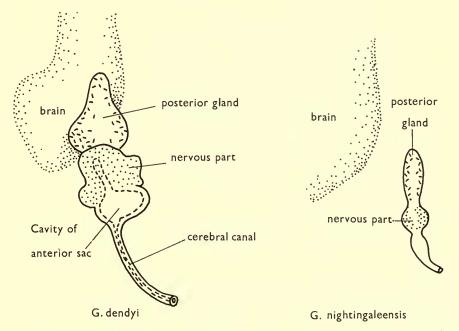
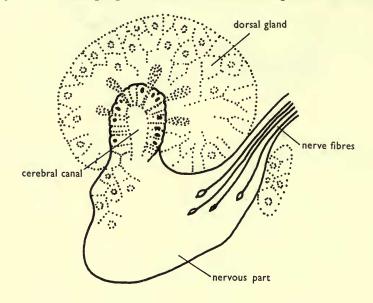


FIG. 3. Cerebral Organs of G. dendyi and G. nightingaleensis in longitudinal section.

6. For most of its course the dorsal blood-vessel of metanemertines runs above the gut and just below the rhynchocoel, but in the neighbourhood of the oesophagus it enters the rhynchocoel and runs along the ventral wall till it leaves the rhynchocoel near the point where the dorsal vessel divides from the cephalic loop. In *G. australiensis* (Dendy, 1892) the dorsal blood-vessel pierces the rhynchocoelic sheath but remains outside the rhynchocoelic cavity. Just behind the ventral cerebral commissure the vessel divides, and its branches supply two curious plugs of tissue which alone separate the blood from the



G. pelaensis FIG. 4. Cerebral Organ of G. pelaensis in transverse section.

rhynchocoel. I have found precisely similar paired structures in G. dendyi supplied by anterior bifurcation of the dorsal vessel (Figs. 14, 15, 16). Hett (1924) notes only one such plug in G. hillii with certainty. Re-examination of her sections shows that here also there are two independent and well-developed plugs. (Owing to slight obliquity of the sections the left-hand plug is in slide "Nem. J.P.H. D6" and the right-hand one in slide "Nem. J.P.H. D7".) Some other nemertines possess rhynchocoelic vascular tissue plugs in the dorsal vessel, but, as in *Prostoma graecense* (see Böhmig, 1898) and in *Prosorhochmus claparedii*, there is only one such plug (Fig. 23, T.S. Prosorhochmus).

- 7. The lateral blood-vessels supply an anastomosing subdermal network of capillary blood-vessels, not the usual quasi-metameric arches of the metanemertine (Fig. 7).
- 8. The nephridia in G. dendyi and G. hillii consist of numerous flame-cells, typically in pairs, situated immediately below the dermal muscle-layer, like

the capillary blood-network. Each flame-cell has a single nucleus at its head, and connects with end canals which join to convoluted common canals, which pass abruptly into second convoluted canals with thick walls of radially organized cytoplasm, and each of which finally empties to the exterior by one

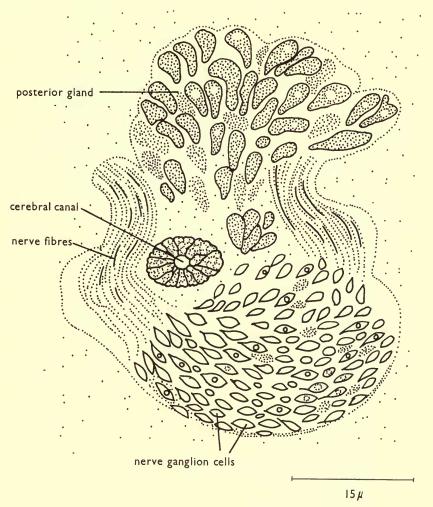


FIG. 5. Longitudinal section cerebral organ of *G. dendyi* to show the appearance of the posterior glandular region.

of extremely numerous nephridial pores over the surface of the animal (Pantin, 1947 : Hett, 1924). Examination of the late Professor Dendy's slides shows that the condition in *G. australiensis* is similar. It is different from that in the freshwater *Prostoma graecense* and from all marine nemertines, including *Prosorhochmus claparedii*.

9. The gut is of the general metanemertine type in which, however, the various

parts are subject to considerable variation. In *G. dendyi* and *G. australiensis* the oesophagus is short and merges into the stomach. The anterior gutcaecum is large and extends forward from the point of entry of the pyloric

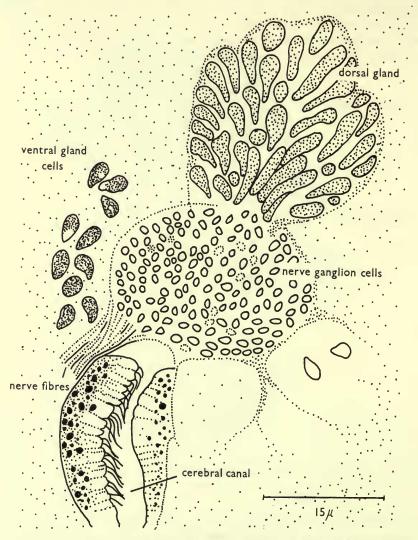


FIG. 6. Transverse section cerebral organ of *G. pelaensis* to show the appearance of the dorsal glandular region. Note beside the cerebral organ the ventral gland cells, cf. dorsal gland cells in *G. dendyi*.

tube into the stomach, and more or less divides into two short branches extending either side of it to the brain. According to Hett (1924), the condition in G. *hillii* is similar to G. *australiensis*. I can confirm the presence of the anterior caecum in G. *hillii*. The condition in these species may be

contrasted with that in the freshwater *Prostoma graecense* in which the caecum is short and gives rise to two long forwardly running branches. (Montgomery, 1895b, and personal observations.)

10. Large specimens are ♀, small ones are ♂ (Fig. 8). In G. dendyi this is apparently due to protandrous hermaphrodity. G. dendyi specimens of intermediate size (3-4 mm.) may have both degenerate testes and mature ova.

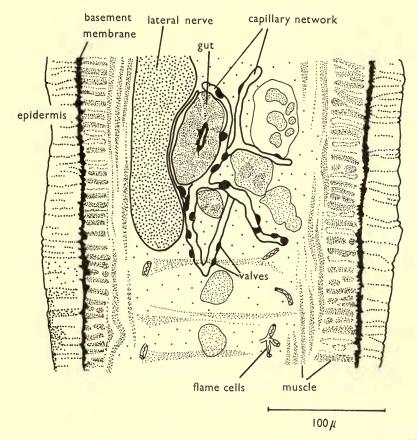


FIG. 7. Longitudinal section G. dendyi to show anastomosing subdermal capillary network.

- **II**. All three species live in similar damp terrestrial situations which may be far from the sea.
- 12. They all occur in southern Australia.

It is evident that these species share many characters which are rare among metanemertines and some which are unique. It is legitimate to infer that they are closely-related species.

The three species are not identical. *G. hillii* differs from the others in the colour pattern (purple brown with two bright red lateral bands in the anterior two-thirds of

the body), and in the very large number of eyes (80). In both the other species the ducts from the cerebral organ open into a transverse cephalic furrow on the ventral surface of the head in front of the brain. This furrow appears to be absent in G. *hillii* (see Hett, 1924). The nephridia are more numerous in this species than in

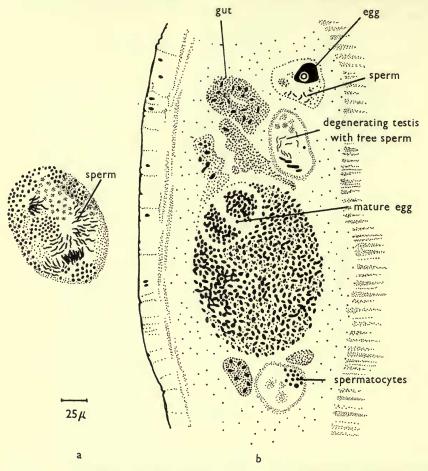


FIG. 8. Horizontal section G. dendyi to show sex organs : (a) mature testis ; (b) degenerating testis and mature ovary.

G. australiensis (see Hett, 1924). It differs from G. dendyi in the large number of stylet-sacs (5 against 2 to 3), the larger number of proboscis-nerves (18 against 11 to 15), and also in the very much more muscular body-wall. Two important distinctions I find between G. hillii and the other two species are the very much larger size of the accessory lateral nerve relative to the size of the lateral nerve itself, and the almost complete absence of the short lateral diverticula, which run forward from the anterior gut caecum to the brain in the other two species.

According to Hett, G. hillii possesses no cephalic gland. But re-examination of

the sections shows distinct though restricted masses of cells possessing the same histology as the cephalic glands in Dendy's original slides of *G. australiensis* (Fig. 9). The difference in development of the gland in the two species is great, and in the specimen of *G. hillii* examined the gland is confined to a dorsal portion behind the brain and two lateral or even ventro-lateral portions in front of it. This is very different from the great dorsal development over the brain in *G. australiensis* or even from the limited similar development I find in *G. dendyi*, but all three species in fact

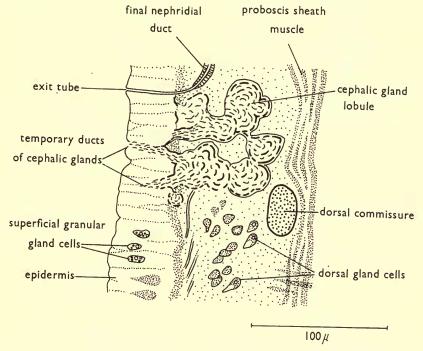


FIG. 9. Longitudinal section *G. dendyi* to show cephalic glands and dorsal gland cells (the bottom of the drawing is anterior).

possess this tissue, and it is similar also to that of the cephalic gland of *G. pelaensis* (see Schröder, 1918). This tissue in *G. australiensis* stains deeply with iron-haematoxylin. The tissue of corresponding structure in Miss Hett's slides does not appear to have done so. Whether this is due to a real difference in nature, or to a difference in the operation of staining, or to the decided variation of state of this gland, such as I have found in *G. dendyi*, remains to be seen, though the latter is the most likely explanation.

G. dendyi and G. australiensis are extremely similar. Many of their quantitative differences, e.g. number of eyes (30-40 in G. australiensis against 10-20 in G. dendyi), the number of stylet-sacs (2-5 against 2-3), the number of proboscis-nerves (16-19 against 11-15), may really be a reflection of the larger size of mature individuals in G. australiensis (up to 40 mm. against 10 to 25 mm.). But they also differ in colour pattern, a median dark brown band with or without slight lateral stripes in G.

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australiensis against two brown lateral stripes only in G. dendyi : as Stephenson points out (1936), while colour may be very variable, pattern is of systematic importance. Further, G. dendyi possesses only a small cephalic gland. Dakin (1915) found none, and Stammer (1934) records it as "kaum entwickelt", but examination of my South Devon specimens shows a limited amount of lobular tissue of the typical large finely-granular secretory cells with small nuclei, which occupies the antero-lateral part of the head just as in the extensive cephalic gland-masses of G. australiensis (Fig. 10). The gland in G. dendyi is much smaller than the extensive

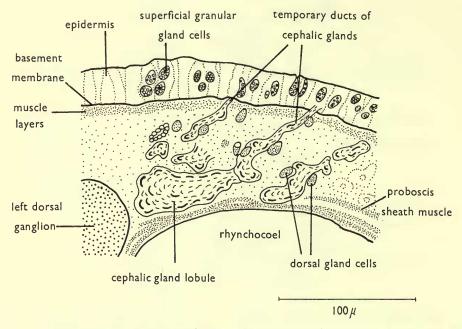


FIG. 10. Transverse section G. dendyi to show cephalic glands and dorsal gland cells (the bottom of the drawing is ventral).

structure figured by Dendy for G. australiensis, but not so much reduced as in G. *hillii*. It was noted that the size of the glandular tissue in G. dendyi varies in individuals, possibly in relation to the amount of recent secretion before fixation. Bürger (1897) has pointed out the relation of these glands to the production of slime round the head in nemertines.

There are other significant quantitative differences to be seen when sections of the two species are compared. In *G. australiensis* the musculature of the body-wall is much more developed than in *G. dendyi*; and though the latter possesses dorsal gland-cells similar to those found in the dorsal part of the head-region of *G. australiensis*, the cells are comparatively few and mostly scattered singly rather than in the well-defined groups figured by Dendy (1892) and clearly to be seen in his slides.

My examination of the three species shows that G. dendyi differs from both the other species in one other important respect. In both the others the posterior

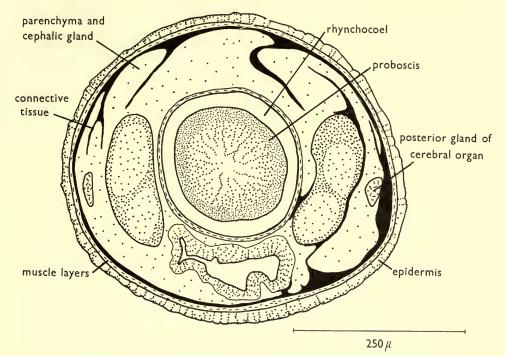


FIG. 11. Transverse section G. dendyi to show position of posterior glandular extension of cerebral organ.

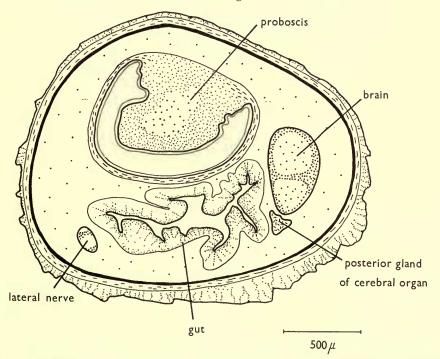


FIG. 12. Transverse section G. hillii to show position of posterior glandular extension of cerebral organ.

glandular extension of the two cerebral organs extends backwards below the beginning of the nerve-cords, so that they lie on each side of the oesophagus and merit Dendy's term "oesophageal organ". But in G. dendyi the extensions run more dorsal and are lateral to the base of the brain (Fig. 11).

From this we may conclude with reasonable certainty that G. australiensis, dendyi and hillii are distinct species of the same genus.

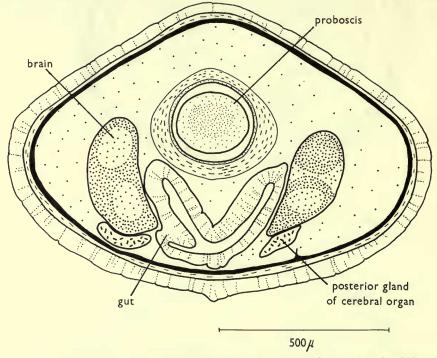


FIG. 13. Transverse section G. australiensis to show position of posterior glandular extension of cerebral organ.

THE PELAENSIS GROUP

Let us now compare the features of the Australian group of species with those of G. pelaensis. This animal has been fully described by Schröder (1918), Hett (1927) and Coe (1940), and I have also been able to examine the slides prepared by Miss Hett and by Dr. Wesley Coe and can confirm the major anatomical characters attributed to the species by these authors. Whilst there is a number of generalized metanemertine characters common to all, G. pelaensis and the Australian group share in addition certain special characters some illustrations of which will be found in Schröder's paper.

1. There is a slight tendency to multiplication of the eyes. The anterior pair remain single and large, but the posterior pair may be divided into two or three pairs of small eyes (Hett, 1927).

- 2. The ducts of the cerebral organ open ventrally into a transverse furrow.
- 3. A mass of gland-cells opens into the posterior, nervous, part of the cerebral organ. From Schröder's figure the cells evidently resemble those of the

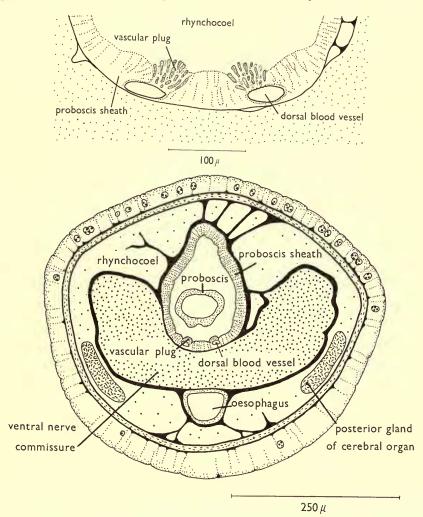


FIG. 14. Transverse section G. dendyi to show the two vascular plugs, from right and left branches of the dorsal blood vessel.

posterior glandular extension of the Australian species, though they are differently situated. I can confirm this (Figs. 4, 5, 6).

- 4. There is an accessory lateral nerve-tract derived from the dorsal ganglion, as in the Australian species, rarely found elsewhere in the phylum.
- 5. As in the Australian species, the dorsal blood-vessel in *G. pelaensis* enters the rhynchocoelic sheath. In this case the dorsal vessel itself carries a plug of tissue which separates it from the cavity of the rhynchocoel. In structure this

plug resembles the paired plugs of the Australian species, but there is only one such plug in *G. pelaensis* (cf. Fig. 17). A similar plug occurs in some other metanemertines, as in *Prostoma graecense* (see Böhmig, 1898) and in *Prosorhochmus claparedii* (Fig. 23).

6. In G. pelaensis, as well as in the Australian species, the protonephridia are extremely numerous throughout the body and, unlike many metanemertines,

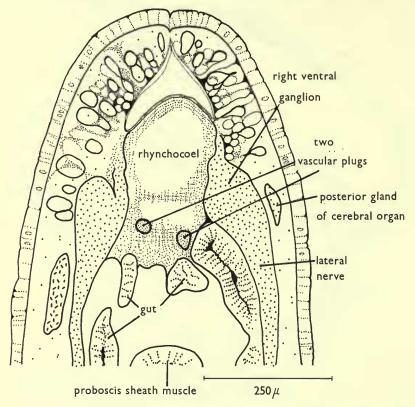


FIG. 15. Longitudinal section G. dendyi to show the two vascular plugs.

are not intimately in contact with the epithelium of the blood-vessels (Schröder, 1918; Coe, 1940), though they may be strongly aggregated in their neighbourhood. Near their exit the excretory canals show striation of the cytoplasm, recalling that of the whole of the last section of the excretory canal in the Australian species. The canals open to the exterior by many thousands of pores all over the surface.

- 7. G. pelaensis is a protandrous hermaphrodite. It undergoes subsequent repeated sex reversals (Coe, 1940); these have not been detected in the Australian species, but may exist.
- 8. G. pelaensis inhabits damp terrestrial situations which may be far from the sea.

These points together, particularly the common possession of an accessory lateral

nerve, lead to the conclusion that there is a significant relationship between G. *pelaensis* and the Australian group.

Geonemertes pelaensis, however, differs from the Australian species very much more than these differ from each other. Some of these differences are due to the retention of generalized metanemertine characters lost in the Australian species.

1. Though there is often some multiplication of the posterior pair of eyes, the eyes are much nearer the primitive tetrastemmatid condition of four eyes.

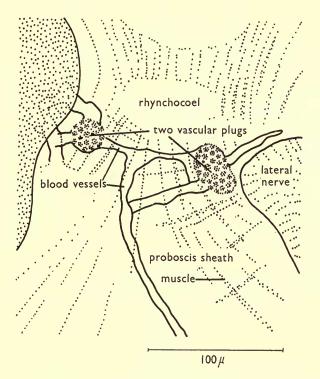


FIG. 16. Longitudinal section G. dendyi to show the two vascular plugs (further enlarged).

- 2. It is to be inferred from Schröder's careful description (p. 161) that *G. pelaensis* lacks "dorsal gland cells" corresponding to those of the Australian species. Schröder (1918) noted, however, the presence of large numbers of gland-cells ventrally and laterally placed in the head, particularly behind the transverse head-furrow. There is none dorsally. I have compared these cells with Dendy's "dorsal gland-cells" in *G. australiensis*, and though their situation and distribution is quite different, the histology of the cells is apparently the same (Fig. 6). The difference thus seems to be one of position and distribution, rather than presence or absence of a particular cell-type.
- 3. The frontal organ as well as the cephalic gland is retained and well developed.
- 4. The vascular system apparently includes commissures between the gut-pouches

(Schröder, 1918), as in many other metanemertines, and does not possess a subdermal plexus as in the Australian species.

- G. pelaensis also differs from the Australian species in specialized characters.
- The posterior glandular part of the cerebral organ does not extend backwards, as in the Australian species. It lies dorsal to the canal in the nervous part of the organ, which it envelops (see Schröder's (1918) figure 39 and see Fig. 4 here).
- 2. Though greatly developed in both in comparison with marine species, the nephridia of *G. pelaensis* differ very considerably from those of the Australian

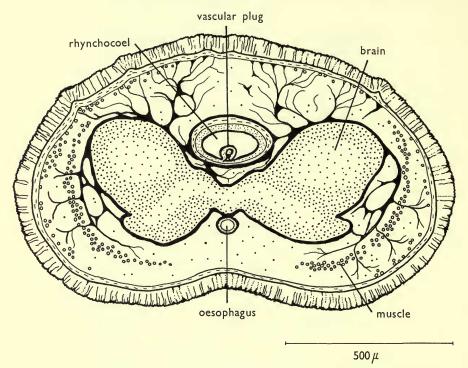
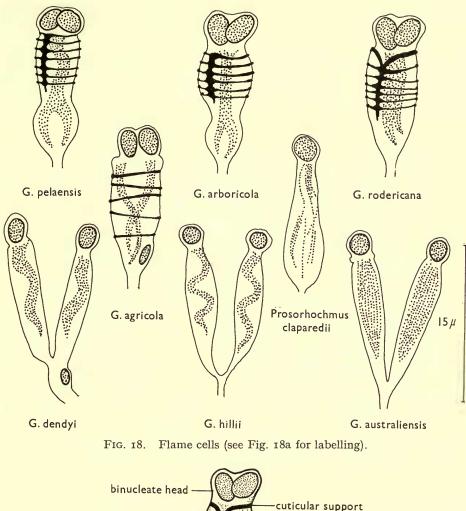


FIG. 17. Transverse section G. arboricola to show the single vascular plug.

species (Fig. 18). The protonephridia do not tend to occur in pairs, but each is itself a double structure. It has *two* nuclei at the head of the ciliary flame instead of one. The cilia of the flame often appear to arise from two roots, one beneath each nucleus. The cytoplasm of these nephridial cells appears rounded, rather than attached to the parenchyma by fine strands as in *G. dendyi*. The upper part of the capsule of the protonephridium is strongly supported by refractile, apparently cuticular, transverse, bar-like structures. Some traces of one or two transverse supporting thickenings of the wall may sometimes be seen under critical optical conditions in the protonephridia of *G. dendyi*, but their development cannot compare with that of the highly developed supporting structures of *G. pelaensis*. These structures consist of some seven strongly developed skeletal rings in the upper half of the protonephridium. The rings are divided



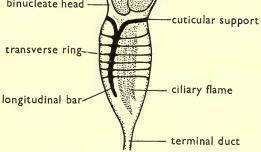


FIG. 18a. G. rodericana flame cell from Fig. 18.

into two halves by two vertical skeletal thickenings diametrically opposite each other in the line of the two nuclei, giving a "bivalve" appearance to the cuticular support (Fig. 18a).

Unlike the condition in the Australian species the protonephridia in *G. pelaensis* are not restricted to a superficial layer in the parenchymal spaces beneath the bodywall. They are found to some extent throughout the parenchyma, even between the rhynchocoel and the gut (Schröder, 1918). Certain parenchymal spaces, particularly along the course of the cephalic vascular loop which runs from the dorsal vessel into the tissue-spaces in the head, are packed with such vast numbers of protonephridia as to constitute "nephridial glands" (Coe, 1940) (Fig. 19). In

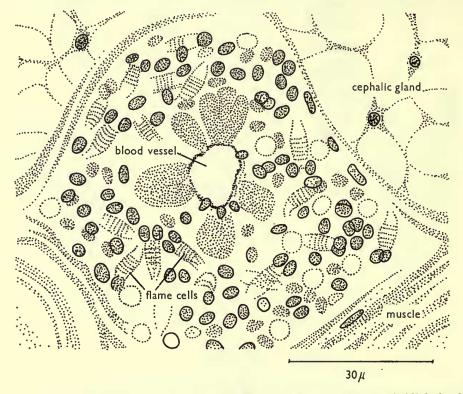


FIG. 19. Transverse section of head region of G. rodericana to show nephridial glands.

contrast, the protonephridia in *G. dendyi* are not directly aggregated round the blood-vessels, though the protonephridia, their ducts, and the superficial vascular plexus of this species are confined to a common layer immediately beneath the muscular body-wall.

Schröder points out (p. 10) that the end-canals of the protonephridia of G. *pelaensis* collect together in tubules following an irregular course. But there is no evidence of the well-defined convolution seen in end-canals of G. *dendyi*. The end-canals of G. *pelaensis* open into tubules with ill-defined walls of vacuolated protoplasm. The tubules lack the striking radial cytoplasmic striation of the second convoluted part of the nephridial canal in G. *dendyi*, and resembles rather the more generalized condition of the tubules in *Prostoma graecense* (Böhmig, 1898, Figs. 19–22) (Fig. 20).

The final relatively short exit canals of *G. pelaensis* do, however, show traces of coiling and also of radial striation (Schröder, 1918), which might perhaps be compared with the much more extensive second convoluted tubule of *G. dendyi*.

Whilst, therefore, there are points of resemblance between G. *pelaensis* and the Australian species, there are some striking differences, particularly in the organization of the nephridial system, which preclude the relation from being a very close one.

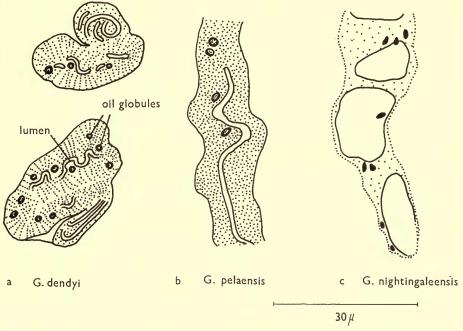


FIG. 20. Nephridial ducts of *G. dendyi*, *G. pelaensis* and *G. nightingaleensis*, showing the thick glandular walls with radial striation in *G. dendyi*.

We shall now pass to two species which prove to be extremely closely related to G. *pelaensis*, notwithstanding wide geographical separation. Geonemertes arboricola was partially described by Punnett (1907) from material collected from the Seychelles on the "Sealark" expedition. He noted some resemblance to G. *pelaensis*, and apart from a supposed absence of nephridia differentiated it only on colour-pattern and the reduction or absence of the posterior pair of eyes. Hett (1927) has pointed out that the examination of further specimens of G. *pelaensis* from Samoa shows that the colour pattern, based in both cases on a single brown dorsal stripe, and eye number of this species is variable and the condition described in G. *arboricola* is within the range of G. *pelaensis*. Punnett, however, found no evidence of an excretory system in G. *arboricola* and did not describe the blood-system.

Specimens and slides of *G. arboricola* in the Cambridge Museum collected on the Sealark expedition were examined. The slides were restained with Mallory's triple stain. Examination showed that *G. arboricola* possesses a well-developed nephridial system and that in this and in other features it resembles *G. pelaensis* very closely :

- 1. As Hett (1927) points out, the colour pattern and eye number of G. arboricola fall within the range of that of G. pelaensis.
- 2. On examination of G. arboricola \overline{I} find that like G. pelaensis it possesses a frontal organ and a well-developed cephalic gland.
- 3. As in *G. pelaensis*, the "dorsal gland cells" of the Australian species are absent in *G. arboricola*, but again we find that there are cells ventro-laterally placed in front of the brain which are not unlike the "dorsal gland cells" in cytology.
- 4. Both species possess a fairly well-developed cerebral organ, which with its gland is nearly as large as the dorsal ganglion. Punnett says the cerebral organ is small, but comparison of his figure (Plate II, Fig. 3) with corresponding slides suggests that he was considering the cross-section of the canal of the organ only. Neither species has the large posterior "oesophageal" gland of Dendy, but both possess similar glandular material above the nervous posterior lobe of the cerebral organ. The ducts from the canal of the cerebral organ open ventrally into a transverse furrow in both cases.
- 5. G. pelaensis is said to have two to four stylet-sacs, whilst Punnett records four in G. arboricola.
- 6. An accessory lateral nerve is present in both.
- 7. G. pelaensis is said to have 16 to 21 proboscis-nerves (Hett, 1927; Coe, 1940). whilst specimens of G. arboricola are described with nineteen.
- 8. Examination shows that, like G. *pelaensis*, G. arboricola lacks a vascular subdermal network but possesses the more generalized lateral commissures running from the dorsal to the lateral blood-vessel between the gut-pouches.
- 9. As in *G. pelaensis*, the dorsal blood-vessel enters the rhynchocoelic sheath and supplies one single plug of cells in the base of the rhynchocoel, just behind the level of the ventral brain-commissure. In *G. arboricola* (Fig. 17) the plug is longitudinally elongated ($40 \times 100 \mu$), and the vessel under the plug bulges into the rhynchocoel much more than do the flat circular plugs of the Australian species.

Schröder's (1918) figure of the plug in *G. pelaensis* suggests that the dorsal vessel ends there. But though rather imperfect fixation of the material I have examined makes satisfactory observation a little difficult, it seems reasonably certain that the dorsal vessel in *G. arboricola* proceeds beyond the plug and branches before the point of entrance of the mouth into the rhynchodaeum. Each branch passes over the lower commissure of the brain and descends to run along the upper surface of the cerebral organ on each side. The branches then run forward towards the snout and, turning upwards, join to form the cephalic vascular loop. I have found a precisely similar system to this showing itself with great clarity in the slides of *G. rodericana* which I have examined (Fig. 22). Examination of Miss Hett's slides of *G. pelaensis* gives a fairly clear indication of the existence of the same arrangement and connexion of the cephalic vascular loop, notwithstanding Schröder's figure.

10. The nephridia of *G. arboricola* agree closely with Schröder's description for *G. pelaensis*. The protonephridia in their upper third have binucleate heads and seven strong transverse supporting half-rings, which connect with stout

vertical bars at opposite sides of the diameter along the line of the two nuclei, (Fig. 18) like those figured by Schröder. The protonephridia freely occupy the parenchymal spaces, and where these are restricted around the cephalic vascular loop by the greatly developed cephalic glands they form "nephridial glands" with vast numbers of protonephridia, as described by Coe (1940) in *G. pelaensis*. In both species the "glands" consist of a dense aggregation of protonephridia along the whole course of the cephalic vascular loop. Reference will be made to this when discussing *G. rodericana*.

In *G. arboricola* and *G. pelaensis* the nephridial end-canal systems are similar. There are numerous wide, highly vacuolated, separate collecting canals which apparently open separately by numerous canals to the exterior. In the Seychelles material the exit-canals can be traced to the basementmembrane, but the fixation of the ectoderm is not sufficiently good to justify with certainty the conclusion that the numerous narrow ducts, which are to be seen in the ectoderm, correspond to the openings of the nephridial exitcanals. The fixation of the specimens is unfortunately too poor to enable detection of any radial structure in the end canals.

- 11. Punnett (1907) states that *G. arboricola* is a simultaneous hermaphrodite. The specimens I have examined appeared to be female. The present evidence allows the possibility that it is a cyclical hermaphrodite like *G. pelaensis*, but does not prove it.
- 12. G. arboricola inhabits damp terrestrial situations which may be far from the sea.
- 13. The recorded sizes are not very different for such a variable character : 35–50 mm. for *G. pelaensis* against 15–25 mm. for *G. arboricola*.

The above observations leave no doubt at all that *G. pelaensis* and *G. arboricola* are very closely related. Indeed there is little anatomical evidence at present to suggest that they are specifically distinct. However, in view of the wide separation between their places of occurrence, in the New Guinea area and the Seychelles, and in view of the possibility that further work, particularly on the relations of the cerebral organ and on the vascular system, may serve to show specific differences, it would lead to confusion if they were now assigned to the same species.

Through the kindness of the authorities of the British Museum (Natural History), London, I have been able to examine material, including original sections, of Gulliver's species of *Geonemertes* (= *Tetrastemma*) rodericana (Gulliver). Gulliver (1879) gave a brief account of this species to which a few points were added by Punnett (1907). The former's account needs correction in that he said that the cerebral organs were absent, and the latter's in that he denied the existence of an excretory system. Both can in fact be demonstrated in the original sections.

G. rodericana is closely related by a number of features to G. pelaensis and G. arboricola. In G. rodericana :

- I. There are two or four eyes (Punnett, 1907).
- 2. The cephalic gland and frontal organ are well developed.
- 3. True "dorsal gland cells" are absent ; though again there are cells of rather similar structure to them in the ventro-lateral region of the head.

- 4. The cerebral organ is similarly placed to that of the other species; it is antero-ventral to the brain and opens by vertical ducts running to a transverse furrow on the ventral surface. There is again no glandular "oesophageal organ" of Dendy, though gland-cells of similar appearance lie above the nervous part of the cerebral organ.
- 5. Gulliver records four stylet-sacs.
- 6. There is an accessory lateral nerve. According to Punnett (1907) the lateral

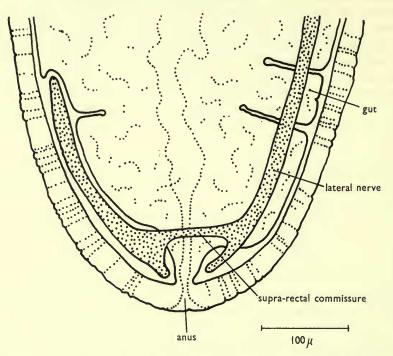


FIG. 21. Horizontal section anal end of G. dendyi to show supra-rectal nerve commissure.

nerves form a posterior supra-anal commissure in this species and in G. *arbori*cola. I can confirm this, but this does not differentiate these species from the Australian species, because there is a small supra-anal commissure in G. *dendyi* (Fig. 21).

- 7. There are 19–21 proboscis-nerves (Punnett, 1907).
- 8. G. rodericana possesses the usual commissural vessels between the dorsal and lateral blood-vessels and does not possess the vascular subdermal network of the Australian group.
- 9. The dorsal blood-vessel enters the rhynchocoel sheath and supplies a single tissue plug in the base of the rhynchocoel just behind the level of the ventral brain-commissure (Fig. 17). It is elongated as in *G. arboricola*, and, as in the latter, the dorsal vessel branches forwards beyond to give the cephalic vascular loop (Fig. 22).

10. The nephridia resemble those of G. pelaensis. The protonephridia have binucleate heads and strong transverse supporting rings divided by two longitudinal bars (Fig. 18). The distribution of the protonephridia in the body is similar to that in G. pelaensis. The canal system resembles that of G. pelaensis.

The relation of the nephridia to the cephalic vascular loop is particularly striking in *G. rodericana*. The loop runs down on each side from the anterior end of the dorsal vessel to the cerebral organ. Each arm then runs forward almost to the anterior end of the head; bends backwards and upwards

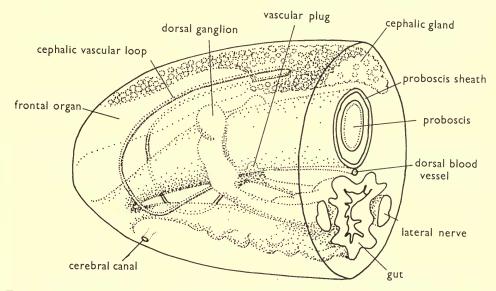


FIG. 22. Reconstruction of anterior end of *G. rodericana* to show cephalic vascular loop (cerebral organs not shown).

through the dorsal part of the head, till they join to complete the loop at a level just behind the brain. Throughout their course the arms of the loop are surrounded by a dense highly localized layer of protonephridia, giving the vessel a very striking appearance (Fig. 19). We have noted that a similar vessel is seen in G. arboricola and G. pelaensis.

Schröder remarks on the close relationship of blood-vessels and protonephridia in the head of *G. pelaensis*, but he seems to consider it as no more than the accidental restriction of both blood vessels and protonephridia to exiguous tissue spaces in the parenchyma. The relation of these structures in *G. rodericana* is far too clear to be accidental : the protonephridia form a dense localized layer round the vessel, which precisely marks its course ; and it is worthy of note that Coe's (1940) figure and description of the condition in *G. pelaensis* suggest a more definite relation than Schröder's account suggests.

It is interesting to note in passing the almost invariable close relationship of the geonemertine vascular system with any structure where much water may be secreted. This is true of the rhynchocoelic cavity, the cerebral organs, the nephridia and also the cephalic gland, alongside of which runs the cephalic vascular loop. The relation suggests that water may be transported to these organs from the body of the parenchyma (cf. Pantin, 1947).

- 11. Punnett (1907) records that G. rodericana occurs as male and female.
- 12. G. rodericana inhabits damp woods. It is killed by immersion in sea water (Gulliver, 1879).
- 13. Punnett (1907) gives its size as 27-75 mm.

The closely similar character of G. rodericana to G. pelaensis is as clear as its difference from the Australian group.

G. rodericana has certain minor points which differentiate it from G. pelaensis and G. arboricola :

- 1. The colour is dark green with a single median white line and four white spots (round the eyes) on the head.
- 2. In the specimens examined the cerebral organs are rather smaller than those of the other two species.

As with *G. arboricola*, the differences of *G. rodericana* from *G. pelaensis* are small and further work is needed to establish the validity of their distinct specific rank, apart from their known minor differences and their widely separate habitat. In any case, the essential similarity of plan in species from widely separate oceanic islands is most remarkable.

G. chalicophora

This species is only known from European greenhouses (Stammer, 1934). Of all the terrestrial nemertines that have been described, *G. chalicophora* has the least number of specialized characters. Böhmig's (1898) description of it is full.

- I. It possesses four eyes, the simple metanemertine condition.
- 2. The cephalic gland is well developed, though as in *G. australiensis* the frontal organ is missing and the gland opens by extempore channels in the dermis of the head. Böhmig makes no reference to structures equivalent to dorsal gland-cells.
- 3. The cerebral organ is well developed, and is similar to that of the freshwater *Prostoma graecense* with which it is compared by Böhmig. Böhmig remarks that in comparison with those of *G. australiensis*, the posterior glands of the cerebral organ are strikingly absent in *G. chalicophora*, though he notes the presence of some such gland-cells in *Prostoma graecense*. The ducts of the organs are rather long $(180 \ \mu)$ and open ventrally, as in all the species so far mentioned, and open directly to the exterior. A transverse head-furrow is not described.
- 4. Like the other *Geonemertes* species we have described, there is an accessory lateral nerve.
- 5. The vascular system retains the quasi-metameric commissures linking the lateral and dorsal vessels and has no subdermal network (v. Graff, 1879).

6. The dorsal vessel enters the muscle of the rhynchocoel, but does not connect with a plug protruding into that cavity. Böhmig contrasts this with the condition of P. graecense which, as he shows, possesses a single plug.

This absence of direct contact between dorsal vessel and rhynchocoel is not very common in metanemertines, but occurs in a few genera, such as *Oerstedia*. Doubtless the absence is a secondary loss.

- 7. The protonephridia are simple structures with one nucleus at the head and no complex skeletal supports. They connect by a system of end-canals with paired lateral longitudinal canals which open to the exterior by some ten orifices on each side, a number far smaller than in any other species of *Geonemertes*. The whole condition is, according to Böhmig, closely comparable to that in *Prostoma graecense* : and, particularly in the unbroken longitudinal canals and in their simple histology, they are much less specialized than anything we have so far seen in *Geonemertes* species. [The flame-cells of *P. graecense* show a tendency which may throw light on the origin of binucleate flame cells like those of *G. pelaensis* ; for Böhmig figures pairs of fused flame-cells with two nuclei at the head, from which arises a double-rooted ciliary flame.]
- 8. Of the sexes little is known. Böhmig only records the presence of females.
- 9. Notwithstanding its lack of special modifications, the animal is well adapted to damp terrestrial conditions, having been found in various European greenhouses though never in the wild state.

The chief characters of *G. chalicophora* which tend to relate it to the Australian and Pelaensis groups are the possession of an accessory lateral nerve (Böhmig, 1898) (Brinkmann points out the common error of its supposed absence in this species) ; and the ventral-running ducts of the cerebral organs. It lacks the other specialized features shared by the two groups. In many points it resembles the New Zealand species and *G. nightingaleensis* : the loss of the vascular plug might be secondary (cf. *Oerstedia* (Stiasny-Wijnhoff, 1930)).

G. agricola

G. agricola has been fully described by Coe (1904). It is to be found in Bermuda only, and I was able to obtain a few preserved specimens collected by Dr. Brian Boden in the summer of 1951. This species has a number of peculiarities, and except on one point my worms agree completely with Coe's excellent description.

In the first place this species has a number of unspecialized features. Among these we may note :

- I. The possession of four eyes.
- 2. The presence of a well-developed frontal organ, as well as a cephalic gland.
- 3. The presence of quasi-metameric commissures between lateral and dorsal blood vessels.

But we are also confronted with a number of striking differences from all the species which we have considered :

- I. The cerebral organs are anterior rather than ventral to the brain, and their ducts open antero-laterally instead of ventrally.
- 2. These ducts open just below a pair of lateral head-furrows which begin from the anterior end at the place where the frontal organ opens into the mouth and rhynchodaeum. As Coe points out, the ducts do not enter these head-furrows. But staining with Mallory's triple stain shows that each opens on to a very shallow channel of specialized ciliated epithelium which stains deep red. This channel continues forward parallel but below the head-furrow and ends before reaching the snout. This is quite a different arrangement from the single ventral transverse furrow of all the other species. But the condition in *G. agricola* is essentially the same as that which I find in *Prosorhochmus claparedii*.
- 3. There is no accessory lateral nerve. Brinkmann points out that Coe's (1904) original account leaves the matter in some doubt, but its absence is clearly shown by Coe both in his Fig. 18 (Plate 25) of a late embryo in his 1904 paper and in his Fig. 4A of an adult in his 1939 paper.
- 4. Coe describes the dorsal blood-vessel as failing to enter the walls of the proboscissheath at any point in its course. I find, however, that at one point just behind the brain it runs for a short distance immediately below the rhynchocoel, and from its upper surface there is a mass of cells histologically comparable to those of the vascular plugs of all other species of *Geonemertes* and also *Prostoma* graecense and *Prosorhochmus claparedii* (Figs. 23 and 24).
- 5. Though a cyclical hermaphrodite (Coe, 1904, 1939), as in *G. pelaensis*, the worm differs from all other species of *Geonemertes* in being viviparous. Again in this it resembles *Prosorhochmus claparedii*.
- 6. The animal, though terrestrial, is confined to the littoral region of the oceanic island of Bermuda (which possesses little natural fresh water). Unlike G. dendyi it is killed by prolonged immersion in fresh water but survives prolonged immersion in sea water (Coe, 1904), and occurs between tide-marks (Crozier, 1917). We may note that *Prosorhochmus claparedii* at Plymouth extends to crevices at the top of the Pelvetia zone, where it accompanies collembolids, myriapods, chernetids and gastropods transitional to land forms.

There seems little doubt in the face of this that G. agricola is widely separated from all other species mentioned and only possesses in common with them all the general metanemertine characters. It might well have evolved the terrestrial habit independently, as Coe (1904) suggests, and this is particularly probable because of its close resemblance to the genus *Prosorhochmus* in precisely those features in which it differs from other *Geonemertes*.

Whilst G. agricola possesses features which serve to remove it from all other species of the genus, it possesses one which remarkably enough it has in common only with the *pelaensis* group. Scattered through the parenchyma are binucleate protonephridia with heavy ring-like cuticular thickenings (Coe, 1929). These thickenings are six to eight in number and are arranged as circular, or possibly spiral, bars at regular intervals across the upper half of the protonephridial chamber. Coe (1929) remarks that these bars extend considerably further down the chamber than in G. *pelaensis*,

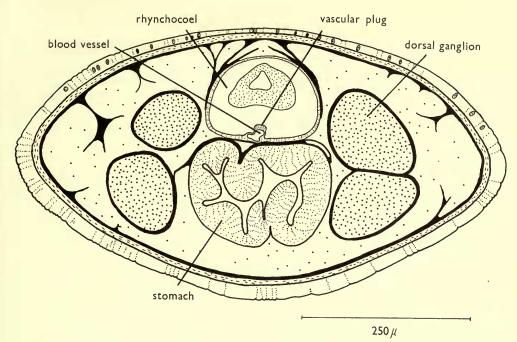


FIG. 23. Transverse section Prosorhochmus claparedii to show the single vascular plug.

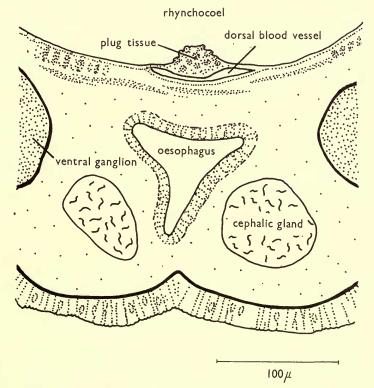


FIG. 24. Transverse section G. agricola to show tissue similar to vascular plug.

and a comparison of his figure with that of Schröder (1918) shows that the bars are much closer together near the head of the protonephridium in *G. pelaensis* (and *G. arboricola*) (Fig. 18). Like *G. pelaensis*, the protonephridia of *G. agricola* may have a longitudinal bar. But there is only one in this case and it is not very prominent. Coe's figures and account do not give the impression of an almost " bivalve " striated structure such as is present in *G. pelaensis* and *G. arboricola*. But in general the resemblance is striking. I can confirm all these observations by direct comparison between *G. agricola* and species of the *pelaensis* group.

The scattered protonephridia occur throughout the parenchymal spaces, including all sides of the proboscis-sheath and the gut. They are most numerous above and below the nerve-cord. Apart from the fact that Coe does not record any great aggregation into "nephridial glands" in the head, the condition seems very like that of *G. pelaensis* and does not show the special restricted sub-dermal distribution of the Australian species.

Coe's (1904 and 1929) accounts of the nephridial system show that this consists of end-canals which unite and join a number of separate convoluted main canals with thick walls. These main canals open to the exterior by some hundreds of openings. These features of the canal system resemble those of *G. pelaensis*, though the resemblance is perhaps rather due to a relative lack of specialization, as compared with the nephridia of the Australian group, than to a unique similarity such as we see in the barred protonephridia. For the canal system resembles in many ways that of *G. chalicophora*, and as Coe (1930) points out is derivable from a general metanemertine condition. The structure of the canal system is not so very different from that of a metanemertine like the freshwater *Prostoma graecense*, except for the break-up of the main canal into separate units and some increase in the number of exit canals (some hundreds), though this is far less than in *pelaensis* or the Australian groups (tens of thousands).

The nephridial canal system in *agricola* resembles also that in *Prosorhochmus claparedii*, except that in the latter the nephridia are confined to the head-region and apparently open by only a few openings on each side. Further, the protonephridia of the *claparedii* are simple and uninucleate (Fig. 18). If *agricola* is truly related to it then, for all their complexity, the occurrence of barred binucleate protonephridia in both *agricola* and *pelaensis* must be accounted convergence.

G. nightingaleensis

There is one other species which has received adequate description, *G. nightingaleensis* Brinkmann. The only important feature which Brinkmann left unstudied was the nephridial system. Through the good offices of Dr. Brinkmann, Mr. Nils Knaben of the Universitets Zoologiske Museum, Oslo, very kindly sent me a specimen of this interesting species collected from Nightingale Island, Tristan da Cunha, by the Norwegian Scientific Expedition, 1937–38. This specimen was sectioned : the anterior end vertically and the remainder transversely and horizontally. In sections stained with Mallory's triple stain, Azan or Masson's Haematoxylin Ponceau-light green method, the major features of the excretory system are clearly brought to light, as is also the circulatory system. The following notes on the anatomy of the species are based on Brinkmann's account and upon these sections.

G. nightingaleensis possesses many unspecialized metanemertine characters and its various characters are shared with other species in a manner not easy to interpret.

- I. It possesses the four tetrastemmatid eyes.
- 2. As in *G. chalicophora* and the Australian group, the frontal organ is lacking and the cephalic gland, which is well developed, opens by many apparently temporary ducts in the dorsal region of the head.
- 3. The cerebral organ is very small, as it is in *G. agricola* (see Coe, 1904), but it is differently situated, being ventral as in the other *Geonemertes* species. But compared with all other species, the organ is very reduced. It is thin $(90 \,\mu \times 20 \,\mu)$, and flattened against the ventral surface of the brain (Fig. 3). The duct is so short that it leads at once into the organ, and there is no obvious cavity corresponding to the anterior sac of the gland, as described by Böhmig in *G. chalicophora* and present in others such as *G. dendyi* (Fig. 3).
- 4. The ducts of the cerebral organ open ventrally as in all species except G. *agricola*, and into a transverse furrow which is incomplete in the middle line.
- 5. There is no accessory lateral nerve. In this the species resembles G. agricola alone.
- 6. The lateral vessel connects with the dorsal by the usual quasi-metameric commissures, which are only found modified in the Australian group.
- 7. The dorsal vessel can be traced to two tissue-plugs in the base of the rhynchocoel near the ventral commissure of the brain. In this the worm specially resembles the Australian species with their two plugs (Fig. 14).
- 8. The protonephridia occur typically in pairs and retain the simple condition with one nucleus in the head and no supporting ribs; as typically in *G. chalicophora* and the Australian group, but unlike *G. agricola* and the Pelaensis group (Fig. 18).
- 9. Unlike the condition in the Australian group, the protonephridia of G. nightingaleensis are scattered through the spaces of the parenchyma. There is, however, a definite tendency for aggregation of protonephridia into a stratum below the muscle-layer. While this slightly recalls the condition in the Australian species there is another feature of the distribution of the protonephridia which calls to mind the condition in the Pelaensis group. The protonephridia tend to be somewhat aggregated round the blood-vessels. There is, however, little or no aggregation round the cephalic vascular loop ; a structure which is rather poorly developed and hard to follow in the specimen I have examined. On the other hand there is a dense aggregation of protonephridia between the base of the brain and the ventral surface, behind the cerebral organ. This is developed about a blood-vessel, which appears to be the anterior end of the lateral vessel, along the whole course of which there is some aggregation of protonephridia. The resemblance to G. pelaensis is thus rather in a general tendency of nephridial aggregation round blood-vessels and not in any specific aggregation round the cephalic vascular loop. A similar

aggregation is seen near the lateral vessels just behind the brain in the *Proso-rhochmus* I have examined.

The end-canal and duct system of the nephridia is less specialized than that in the Pelaensis group, and much less so than that of the Australian species. It recalls rather the condition in *G. chalicophora* and in *G. agricola*, the endcanals joining to form irregular coils which open into one of a number of fairly thick-walled coiled main canals which pass to the body-wall and empty by numerous pores to the exterior (Fig. 20). Altogether the whole excretory system resembles the relatively unspecialized condition in *G. chalicophora* rather than any other species.

- 10. The animals have either separate sexes or are perhaps protandrous hermaphrodites.
- 11. As in *G. agricola*, the species inhabits a region just above the tide level, and resembles it also in being found on an isolated island in the Atlantic Ocean (Nightingale Island, Tristan da Cunha).

This species brings out clearly the most puzzling features in the genus. Apart from the evident close relation of the species respectively within the Australian and Pelaensis groups, it is scarcely possible to find any major characters which divide the group in a way consistent with a division based on any other major character.

G. novaezealandiae

[See Appendix, where the author's draft has been expanded to include subsequent information. Ed.]

G. graffi, G. spirospermia and G. caeca

It is not intended to discuss in detail the remaining species since their descriptions are quite inadequate. G. graffi (Bürger, 1896) and G. spirospermia (Darbishire, 1909) possess four simple eyes and are believed to have an accessory lateral nerve. These are points in common with the *pelaensis* group and G. chalicophora. But without knowledge of the vascular and excretory systems no more can be said ; and Darbishire's description of the accessory lateral nerve as "a ganglionic strand running along the dorsal surface of the nerve-cord" raises the suspicion that he was really referring merely to the normal dorsal layer of ganglion-cells of the lateral nerve itself. The question must be left in this vexing position till we have more material. Nothing is known of G. caeca (Darbishire, 1909) which would enable a new organism certainly to be identified as belonging to this species.

DISCUSSION

We now possess sufficient knowledge of ten of the species of the genus to permit us to consider their relationship. It is clear that *G. pelaensis*, *G. arboricola* and *G. rodericana* on the one hand and *G. dendyi*, *G. australiensis* and *G. hillii* on the other form each of two very closely related groups of species. The two groups show a limited resemblance to each other. What is known of *G. novaezealandiae* (see Appendix) strongly suggests close relation with the Australian group. The relation of the *pelaensis* and Australian groups to the remaining species is, however, very curious.

The following table shows the distribution of the characters common to more than one species or group of species. The retention of a morphological character in the generalized metanemertine condition is represented by O. The suppression of such a character is represented by — and the appearance of a new or modified character by +. Special characters restricted to one species or group alone are not shown.

There are several clear morphological characters which could be used to divide the group, but the resulting divisions are mutually inconsistent. All the Indopacific species have an accessory lateral nerve. The presence of such a tract is of great morphological significance. When the complex relations of a nervous structure to sensory and motor organization are considered it is evident that the chance of the independent evolution of such a structure is much less than that of what may be a genetically simple character, such as colour-pattern or the mere suppression of a structure like the frontal organ. It should, however, be remembered that the degree of development of the tract varies greatly. It becomes steadily reduced as we pass back along the body of the animal. And at any level it is more highly developed in some species than in others ; compare its weak development in *G. dendyi* with the strong development in *G. hillii* (Fig. 2, just before the anterior end of the gut caecum). [See Appendix for re-assessment of this character].

Whilst the presence of an accessory lateral nerve separates the Indo-pacific from the Atlantic species, other characters cut across this division. A number of characters distinctive of the Australian group are to be found in *G. nightingaleensis*; notably the simple nephridia, the absence of the frontal organ and in particular, the double rhynchocoelic vascular plugs. The *pelaensis* group does not share these characters. Still more remarkable the *pelaensis* group of the Indo-pacific appears to share two characters with *G. agricola* from Bermuda alone. The retention of the frontal organ is not very remarkable as a common feature ; but the presence in both of binucleate flame-cells with skeletal supporting bars is very strange, and especially so because in every other respect *G. agricola* stands far apart from all the other species.

Nor do our difficulties end here, for when to the others we try to relate G. chalicophora, that species of unknown origin and of many generalized characters, we find further inconsistencies. G. chalicophora differs from G. nightingaleensis in that the dorsal vessel does not form any vascular plugs in the rhynchocoel, let alone a pair after the Australian pattern. It is thus presumably more generalized than G. nightingaleensis. But on the other hand it already possesses the accessory lateral nerve which is not to be found in that species.

If we attempt to make a "natural" classification on traditional evolutionary lines we find that whichever way we make it we have to assume that more than one character has been independently evolved. We might for example suggest that *G. agricola* is distinguished from the other species by so many features that it is probable that its binucleate barred flame-cells are evolved independently from those of the *pelaensis* group. One might point to the parallel of the nematocysts of

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SUMMARY OF GEONEMERTINE CHARACTERS (including material from Appendix)

--- suppression of character. 0 = retention of primitive Metanemertine state. + = special Geonemertine character.

No of stylet sacs	8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8
No. of proboscis nerves	19 12 15 13 13 10 17 13 10 19 16 10 19 10 10 10 10
Ассеязогу lateral nerve (+)	0+00+++000
Frontal organ	0000
" Australian " nephridial " ducts (+)	000+++0000
Binucleate flame cells with skeletal bars (+)	000000++00
Capillary network (+) or metameric commissures (O)	00++++00
(o, 1 or 2) (o, 1 or 2)	кокакинни
Cephalic furrow transverse (+)	++++++000
Canal of cerebral organ Ventral (+) or Lateral (O)	++++++000
(+) səyə to notsəilqitluM	00000+5000
Viviparous (V) or Oviparous (O)	000000000000000000000000000000000000000
Terrestrial (T), Littoral (L) or Freshwater (FW)	нечеееечь В
Indopacific (I), Atlantic (A) or Southern (S)	х Х А Ч Ч К № № № № № № № № № № № № № № № № №
	 G. nightingaleensis G. chalicophora G. chalicophora Acteonemetres bathamae G. novaezealandiae G. novaezealandiae G. pantini Australian group Pelaensis group G. agricola Prosorhochmus claparedii Prostoma graecense

coelenterates and of protozoa like Epistylis as an example of the relative ease of independent evolution of complex structures at the cellular level. But this would still leave us with the duty of relating G. nightingaleensis and G. chalicophora to the Indo-pacific species. If we start from the resemblance between the somewhat generalized G. nightingaleensis and the Australian species, we must account for their relation to the pelaensis group either by assuming that G. nightingaleensis has secondarily lost the accessory lateral nerve or that the pelaensis group which already possesses this structure has secondarily acquired its single rhynchocoelic vascular plug from the double condition seen in G. nightingaleensis and the Australian species. Any alternative starting point involves us equally in a number of additional assumptions. Each additional assumption weakens the force of an inductive argument for relationship.

It is, of course, quite clear that several of the characters we have discussed must in fact have been evolved independently. The difficulty in this elegant puzzle is to assess which characters can be assigned the lowest probability of independent evolution. That assessment can only be made when we have far more knowledge of those generalized littoral Tetrastemmatidae and Prosorhochmidae to which the Geonemertines are evidently related. For it is on the range and character of variation in these that our assessment of relationship must rest. The consideration of the relationship of the Geonemertine species brings out very clearly the tentative character of any "natural" classification. The arguments in favour of such classifications are in fact subjective estimates of probability and their weight must necessarily vary continually with the extent of contemporary knowledge.

But notwithstanding the uncertainty attaching to the relationship of the Geonemertine species it is certain that some characters here defined must have been independently evolved by different members. This is the more remarkable in view of the rigidity of plan of metanemertine organization ; a rigidity which is so great that it would be difficult for anyone, other than a specialist, when presented with a preserved specimen of a Geonemertine to detect any fundamental departure in organization from its marine relatives—or indeed to infer that it was not a marine, but actually a terrestrial organism.

With these qualifications we may provisionally classify the species of the genus dealt with herein as follows:

Genus Geonemertes I. Fully terrestrial With accessory lateral nerve With ventral cephalic furrows With dorsal blood-vessel entering rhynchocoelic sheath I.I. With uninucleate flame cells without skeletal bars Without multiplication of eyes Without rhynchocoelic plug Without frontal organ With few nephridial openings (about IO) (European greenhouses) G. chalicophora. v. Graff, 1879.

1.2. With rhynchocoelic plug

With thousands of nephridial openings.

- 1.2.1. Without or with slight multiplication of eyes With frontal organ
 - With hontal organ
 - With binucleate flame cells with skeletal bars
 - With " nephridial glands " round the cephalic blood vessel
 - With single rhynchocoelic vascular plug.
 - 1.2.1.1. Red, with dark brown dorsal stripe. New Guinea. G. pelaensis. Semper, 1863.
 - 1.2.1.2. Seychelles. G. arboricola. Punnett, 1907.
 - 1.2.1.3. Dark green with single median white line. Rodriguez. G. rodericana. Gulliver, 1879.
- 1.2.2. Without frontal organ
 - With uninucleate protonephridia without bars
 - With two rhynchocoelic vascular plugs
 - With multiple eyes
 - With posterior extension of glands of the cerebral organ
 - With complex nephridial ducts and radial striation
 - With vascular subdermal network.
 - 1.2.2.1. With posterior extension of glands of cerebral organ on either side of oesophagus (" oesophageal organ " of Dendy).
 - I.2.2.I.I. With cephalic gland poorly developed and absent over brain. New South Wales. *G. hillii*. Hett, 1924.
 - 1.2.2.1.2. With well-developed cephalic gland. South-eastern Australia, Tasmania. *G. australiensis*. Dendy, 1889.
 - 1.2.2.2. With posterior extension of glands of cerebral organ lateral to brain

With relatively small accessory lateral nerve

South-west Australia. G. dendyi. Dakin, 1915.

2. Littoral

Without accessory lateral nerve

2.1. With uninucleate protonephridia without bars Without ventral cephalic furrow With dorsal blood-vessel entering rhynchocoelic sheath Without frontal organ With two rhynchocoelic vascular plugs. Nightingale Island. G. nightingaleensis. Brinkman, 1947.

2.2. With antero-lateral cephalic furrows Without dorsal blood vessel in rhynchocoelic sheath With binucleate flame cells with skeletal bars With frontal organ

Viviparous. Bermuda. G. agricola. Willemoes-Suhm, 1874.

It is a pleasure to express my thanks to the many persons I have mentioned through whose kindness I had access to material from many species, and I must particularly thank Dr. Brian Boden, Dr. August Brinkmann, Dr. Wesley Coe, Miss M. Hett, Professor Doris Mackinnon and authorities of the British Museum (Natural History).

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APPENDIX

By JANET MOORE

Reason for deferred publication

The above paper dates from 1952. The reason for delay in publication is clear from Dr. Pantin's correspondence: "The draft is not final because after my visit to New Zealand, when I'd found *Geonemertes novaezealandiae* and *Acteonemertes bathamae*, I came to the conclusion that my divisions were on the right lines but there was still more to say, particularly about my new shore species and a redescription of *novaezealandiae* itself" (Letter to F. Crandall (University of California), May 1959). And later, "... not yet published. That is largely because I've got a very great deal more information about the New Zealand species and other species from elsewhere in the world" (Letter to Professor A. Stock, (Armidale, New South Wales), December 1962).

In 1961, however, Dr. Pantin published his Presidential Address to the Linnean Society "Geonemertes : A Study in Island Life" (Pantin, 1961a) and also "Acteonemertes bathamae, Gen. et. Sp. Nov. An Upper Littoral Nemertine from Portobello, New Zealand" (Pantin, 1961b). The first of these papers gives a preliminary report on some of the findings described in the present paper. Letters from Dr. Pantin establish that this was not intended to be a substitute for the present paper. It was written before further findings were made during Dr. Pantin's 1961 visit to New Zealand.

THE NEW ZEALAND GROUP

Referring to the present paper, Dr. Pantin wrote to F. Crandall in August 1959: "It was written before I had studied the *Geonemertes pantini* sections and the *G. novaezealandiae* material. It was also before I had looked at my new undescribed shore nemertine, which seems closely related to the New Zealand and Australian species. ... My ideas have gone a good deal further since I wrote it because it was written before I went to New Zealand." (This refers to the 1954 visit : the 1961 visit produced yet more data.) Accordingly, in the present form of the paper the earlier brief account of *G. novaezealandiae* (based on restaining of slides in the collection of the late Professor Dendy) has been deleted. The following expanded version includes the second species found in New Zealand, *Geonemertes pantini* Southgate (Southgate, 1954). The account is derived from Dr. Pantin's notes on his own specimens and interpreted by study of the slides prepared from them for him by Mr. D. Buck of the Zoology Department, Cambridge.

A. G. novaezealandiae

- 1. The colour pattern consists of four dark brown dorsal bands on a cream background. The two median bands are wider and more pronounced than the two more lateral stripes (see Frontispiece).
- 2. There are four eyes, two large and two small.

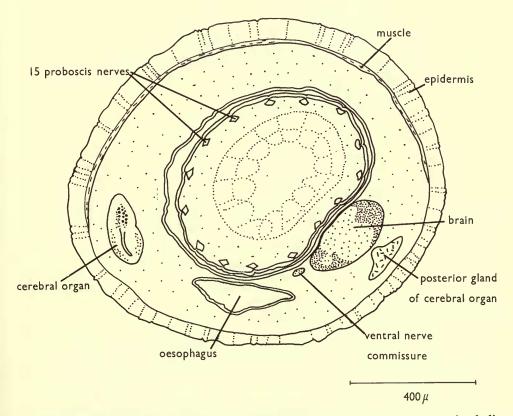


FIG. 25. Oblique transverse section G. novaezealandiae to show cerebral organ (cephalic gland not shown).

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- 3. As in the Australian group, it lacks a frontal organ, though it possesses a cephalic gland. There are improvised channels for escape of the secretion.
- 4. The cerebral organs and their ducts are ventral and open ventrally (see Fig. 25). [There is a posterior glandular extension of the cerebral organ as in the Australian group, but it is shorter, extending backward only to anterior brain level. The extension is not as dorsal and lateral in position as in *G. dendyi* (Fig. 11). J.M.]

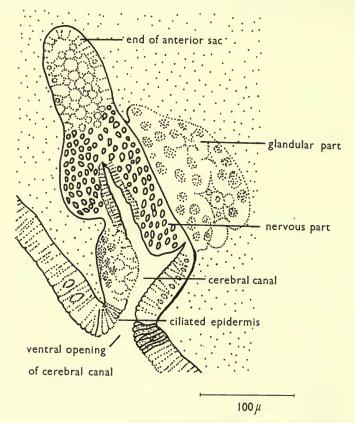


FIG. 26. Cerebral organ of G. pantini.

- 5. There are four stylet sacs.
- 6. There are 13–17 proboscis nerves.
- 7. There are two rhynchocoelic plugs from the dorsal vessel and there is a network of capillary blood vessels as in the Australian Group (cf. Figs. 14 and 7).
- 8. The protonephridia are uninucleate and without bars. The remainder of the nephridial system also is exactly similar to that in the Australian group, the glandular canals having thick walls with radial striations (Fig. 27).
- 9. Unlike both the Australian group and the *pelaensis* group, G. novaezealandiae has no accessory lateral nerve (Fig. 28).

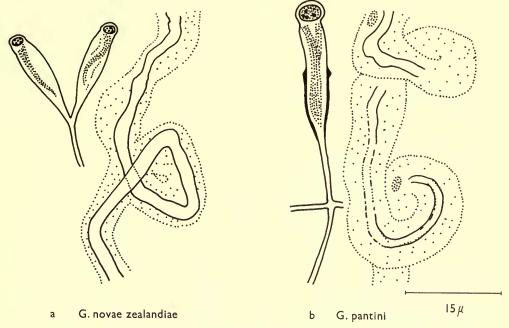


FIG. 27. Flame cells (on left) and nephridial ducts (on right) of G. novaezealandiae and G. pantini.

B. G. pantini

The above description of G. novaezealandiae applies exactly to G. pantini except that :

- I. G. pantini has two warm brown stripes (see Frontispiece) of a different brown pigment, probably a melanin. "The pigment of G. novaezealandiae is either a porphyrin or near that chemically, while G. pantini has a different pigment—more insoluble. (This could be little more than a varietal difference perhaps—though it may prove to be more)." (Dr. Pantin to Mr. Southgate (Dunedin), 19th November, 1961.)
- 2. The accessory lateral nerve is present in *G. pantini* (see Fig. 28). "In all the specimens I have cut of either [*G. novaezealandiae* or *G. pantini*] the results are that so far as I can see they agree with each other in all their special characters which are shared with the Australian species, but like *Acteonemertes, novaezealandiae* has no accessory lateral nerve while *pantini* undoubtedly has one, just as in your type. This is quite extraordinary and has all sorts of implications" (Dr. Pantin to Mr. Southgate, 22nd November, 1961).

Southgate (1954) reports no accessory lateral nerve in G. *pantini*. This is because originally he followed Darbishire in considering the accessory lateral nerve to be a separate and distinct structure, instead of a separate tract of

nerve fibres within the main bundle. He later entirely agreed with Dr. Pantin's account.

3. "Another feature which I noticed in your type *pantini* was that the longitudinal muscle is organized into well-defined bundles, and I have not yet seen this to be the case in *novaezealandiae*. That might simply be due to the fact that your type specimen of *pantini* was a very fine large animal and the musculature may get more organized as an animal grows bigger " (Dr. Pantin to Mr. Southgate, 2nd August, 1960).

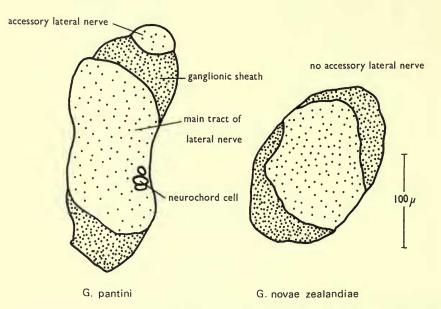


FIG. 28. Lateral nerves of *G. pantini* and *G. novaezealandiae* at the level of the first appearance of the anterior gut diverticulum (both figures show the nerve on the left of the section, with dorsal surface uppermost).

[Bearing out this last suggestion, there are sections of a very small specimen . . . "which because of its colour pattern I called *G. pantini* when I collected it ". This has a small accessory lateral nerve, but does not have its longitudinal muscle in well-defined bundles. J.M.]

That the accessory lateral nerve was absent in *G. novaezealandiae* and present in *G. pantini* removed all doubt that these were two distinct species. On the contrary, "This is quite astonishing for a specific difference—it is more like a familial character" (Dr. Pantin to Mr. Southgate, 19th November, 1961).

"... it might suggest that the accessory lateral nerve was only evolved during the radiation of the *novaezealandiae* species. The alternative that G. *pantini* and G. *novaezealandiae* are very distantly related must, I think, be ruled out because of the very numerous other similarities of vascular system, nephridia and the rest which they possess " (Dr. Pantin to Mr. Southgate, 2nd August, 1960). [In one specimen of *G. pantini*, the accessory lateral nerve becomes separated from the main lateral nerve and follows a separate course for some 200μ , and then rejoins the main tract. This happens twice on the same side. During the separation, the lateral nerve cord looks just like that of *G. novaezealandiae*. J.M.]

The whole question of the significance of this character is brought in question by these two New Zealand species (see also the discussion in the main body of the paper).

"There is I think much more difference between these two species than I had first supposed, or this character is much more variable than people have generally believed and taken for granted. The answer of course will not come until I have been able to cut many specimens" (Dr. Pantin to Dr. V. V. Hickman (Tasmania), 27th October, 1961). Dr. Pantin's latest comment on the situation is: "In general the striping in the New Zealand species is certainly much more pronounced than in the Australian ones. Within the colour pattern of *G. novaezealandiae* there is certainly variation, though the underlying features of the pattern always seem to remain. However, quite apart from the variability within the pattern, there are, I am sure, real specific and subspecific differences (e.g. the presence of an accessory lateral nerve in *pantini* and its absence in *novaezealandiae*). Therefore I have paid particular attention to getting material from type localities" (Dr. Pantin to Dr. V. V. Hickman, 22nd January, 1963).

Localities where G. novaezealandiae and G. pantini were found should be recorded :

- G. novaezealandiae
 - (a) Toi toi, Fortrose, Nr. Invercargill, Southland, N.Z. A deserted farmhouse 3 miles south of Waimahaka on the road to Fortrose. This is a type locality (Dendy, 1895). Dr. Pantin found specimens there in 1954, but in 1961 the place was found to be unfenced and ruined by sheep.
 - (b) Tokanui, Nr. Invercargill, Southland, N.Z. A wood 1¹/₂ miles south east of Tokanui station ; a small patch of bush on the slopes of a hill. Specimens were in crevices and hollows in rotten trunks of tree ferns. (Dr. Pantin, Dr. Henry Pantin, Dr. E. J. Batham and Mr. Southgate, August 1961).
 - (c) Mount Somers, near Ashburton, Canterbury, N.Z. In decomposing timber near the edge of Alford Forest at the foot of Mount Somers. Type locality (Dendy, 1895). Dr. P. M. Johns and Dr. Pantin, August 1961.
 - (d) Signal Hill, Dunedin, N.Z. Dr. Pantin and Dr. E. J. Batham, 1961, but "I am not sure that the few "G.n.z." specimens from Signal Hill really are G.n.z. and not just a colour variety of G. pantini" (Dr. Pantin to Dr. Batham (Portobello Marine Station), 19th November, 1961).

G. pantini

- (a) Signal Hill, Dunedin, N.Z. Type locality, (Southgate, 1954). Subsequently also found by Dr. Pantin and Dr. Batham.
- (b) Leith Valley, near Dunedin (Dr. Pantin, 1954).
- (c) Taupo, North Island, N.Z. (Dr. P. M. Johns, 1961).

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C. The Menzies Bay Geonemertine

In 1961 Mrs. Allison from Christchurch (University of Canterbury) took Dr. Pantin to Menzies Bay (Banks Peninsula, South Island) where she had found a small land nemertine, and Dr. Pantin found three more specimens : "It looks very different from any of the others—possibly because they were small and perhaps immature but I suspect a different species " (Dr. Pantin to Mr. Southgate, 15th August, 1961). One specimen was only 10 mm. long, with the dorsal surface mottled brown with a clear line over the proboscis, and only two eyes seen with a hand lens. These specimens were never sectioned, but are preserved in the Cambridge Zoology Department.

D. Acteonemertes bathamae

This new species was described by Dr. Pantin (1961b). It is an upper littoral marine worm which occurs on the Portobello Peninsula, South Island, and other sites in New Zealand. Its chief interest lies in its close similarity to the Australian and New Zealand species of *Geonemertes*, despite its littoral habit. It lacks an accessory lateral nerve, differing in this way from all these *Geonemertes* species other than *G. novaezealandiae*. There is, however, a small contribution from the dorsal ganglion to the main lateral nerve (Pantin, 1961b).

E. G. spirospermia and G. caeca

Two more New Zealand species of *Geonemertes* have been described, *G. spiro-spermia* and *G. caeca*, from the sub-antarctic Auckland and Enderby Islands (Darbishire, 1909). These descriptions are quite inadequate (see main paper). Dr. Pantin hunted in vain for Darbishire's specimens, and never examined any specimens from the outlying islands (some were kindly sent, latterly, by Dr. P. M. Johns of the University of Canterbury, Christchurch).

THE AUSTRALIAN GROUP

Dr. Pantin had intended to search for geonemertines in Australia, with particular attention to specimens from type localities.

G. hillii was sent to him by Professor A. Stock of the University of New England, Armidale, New South Wales. The orange pigment was analysed by Dr. V. H. Booth and found to be an unknown carotenoid, possibly astaxanthin. Professor Stock defines the distribution of G. hillii in New South Wales as follows (letter to J. M., 1st February, 1968) : "We found G. hillii in a locality (Point Lookout) "—about 50 miles due east of Armidale—" at an altitude of about 5,000 ft. in a relatively dry situation. Since then we have found it near a place called Dorrigo (Dorrigo National Park) at an altitude of 2,400 ft. and at the edge of a rain forest and lately at the foot of Dorrigo Mountain, at 500 ft. in subtropical rain forest on the upper reaches of the Bellinger river (Bellinger river, North arm). This extends the range to the east to the edge of the coastal plain and fits in with Fletcher's (1891) find in a similar situation on the Richmond river. "The crest of the mountain chain along the eastern coast of New South Wales seems, as far as we know at present, to be the limit to the west of the distribution of G. hillii."

G. australiensis has not been found in recent years at Dendy's original site in New South Wales, but has been obtained from Victoria. Specimens from Tasmania were sent to Dr. Pantin by Dr. V. V. Hickman, and these do not differ specifically from the Victorian specimens (Hickman, 1963).

Dr. Hickman has examined a large number of specimens (187 adults and 374 young) and has found a much greater range of variation than was previously recorded for the species :

Size : Males 12-60 mm., females 12-84 mm., in length (Dendy recorded " up to 40 mm.").

No. of proboscis nerves : 11-21, most often 14 (Dendy, 16-19).

No. of reserve stylet sacs : 2-II (Dendy, 2-5).

No. of eyes : up to 170 (Dendy, 30-40, and G. hillii with 80 eyes was distinguished as having more than G. australiensis (Hett, 1924).

The colour varied from pale cream to dark reddish brown, and there was in particular variation in the degree of striping, previously considered to be an important distinguishing characteristic (Stammer, 1934). The colour may be uniform (striped and non-striped specimens may occur in the same habitat) or there may be irregular brown blotches on a cream to pale brown background. Most commonly there is a single median dorsal stripe, with or without a lateral stripe on each side, or the median stripe may be double, giving four longitudinal stripes (Hickman, 1963).

MADEIRA—THE AZORES. G. chalicophora?

"I have just come back from Sweden with a collection of worms from the Azores and from Madeira which Professor Dahl believes may be identical with *G. chalicophora*, the one remaining species of uncertain origin " (Dr. Pantin to Mr. Southgate, 19th December, 1961).

Professor Dahl has very kindly suggested that these slides should remain in Dr. Pantin's collection. He writes : "I was very much in doubt whether they should be regarded as *G. chalicophora* or whether they should be regarded as a new species, although I was more in favour of the first alternative. We spent most of a day over the slides and over material which Professor Pantin had brought without being able to make up our minds. However, I do think that we both tended rather to lump them with *G. chalicophora*" (Professor Dahl (University of Lund) to J.M., 20th December, 1967).

The exact localities are also recorded for all Professor Dahl's *Geonemertes* in Madeira and the Azores. No land nemertines have since been received from these islands.

THE MAURITIUS SPECIES

Land nemertines were sent to Dr. Pantin in 1962 by the late Dr. Vinson, Director

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of the Mauritius Institute. These worms were found under a large stone in the dry zone of the coastal belt, "Roches Noires", and in very damp situations of the uplands.

"The structure is most interesting. It is quite clear that your worms belong to the same group which extends through from the Seychelles across the Indian Ocean to Samoa. They have all the proper features which put them in this group " (i.e the Pelaensis group)—(Dr. Pantin to Dr. Vinson, 14th June, 1962).

"It would take me a little time to get round to sectioning the worms and describing them, but when I do, I should like to call this species GEONEMERTES VINSONI—if you would let me do so " (Dr. Pantin to Dr. Vinson, 27th August, 1963).

MISCELLANY

(a) Recommended method of fixation

Dr. Pantin found the best fixatives to be Susa or 80% ethyl alcohol. These methods, followed by a polychrome stain such as Mallory's triple stain or Masson's haematoxylin-Ponceau-light green, were best for bringing out details of the excretory and vascular systems. Fixatives containing acetic acid, and Bouin, should be avoided.

Two alternative prescriptions which he gave in recent years (kindly supplied by Dr. S. A. Corbet) were :

- (i) 7% ethyl alcohol until movement almost stops 80% ethyl alcohol to kill and fix 80% ethyl alcohol+5% glycerine to preserve the worms
 (ii) 7% ethyl alcohol to anaesthetize the worms
- Susa fixation 90% alcohol+iodine 90% alcohol (store in methyl benzoate).

 (b) Negative Records : places searched for Geonemertes without success : Brazil (Dr. Pantin) Hawaii (Dr. Pantin, 1961) Canary Islands (Tenerife and Gomera) (Dr. S. A. Corbet, 1964)

St. Helena (Mr. A. Loveridge, 1966).

(c) Incompletely documented species

In addition to G. spirospermia and G. caeca from New Zealand, there is another inadequately described species, G. graffi (Bürger, 1896) also referred to as G. micholitzi, or G. stamarai. This species occurs in New Guinea. There are no certain differences from G. pelaensis.

There is also a fragment of a geonemertine in the Cambridge Zoology Museum marked "Peradeniya". (It is included as such on the world map in Pantin (1961a) with no explanation.) This specimen was collected by Dr. Punnett in Ceylon in 1909, but it could never be further traced. Dr. Pantin records "... unquestionably closely related to *G. pelaensis*. It has six eyes, a single vascular rhynchocoelic plug, and above all the typical barred, binucleate protonephridia" (Dr. Pantin to Mr. Prudhoe, 28th January, 1952).